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Caspian Tern Predation on Salmon and Steelhead Smolts in the Columbia River Estuary

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National Marine Fisheries Service
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Caspian tern - Dr. Dan Roby
juvenile *Oncorhynchus mykiss* - Dr. Ernest Keeley
Caspian Tern with fish - Columbia Bird Research Team

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Executive Summary

- Human activities have contributed to salmon and steelhead population declines in the Columbia River Basin.
- Predation by Caspian terns living on constructed islands in the Columbia River estuary is a relatively new source of juvenile salmonid mortality.
- The effect of Caspian tern predation varies between years and amongst salmonid species and is greatest on steelhead and smallest on wild yearling chinook.
- Caspian tern predation on juvenile salmonids significantly affects recovery, however removing all tern predation will not, by itself, lead to full recovery of any listed salmon and steelhead stock.
- The effect of Caspian tern predation on recovery may be comparable to fish passage improvements at Columbia River dams and harvest reductions for some ESUs.
- Moving Caspian terns to habitat that offers a greater diversity of prey can reduce the impact predation has on juvenile salmonids.
- Returning the estuary to a more "normative" process is likely to allow for a more diverse diet for Caspian terns, reduce predation pressure on salmonids and provide better habitat for a wide variety of animals as well as juvenile salmonids.

Background

A common axiom among Northwest salmon managers is that the number of salmonid adults recruited is a positive response to the number of smolts produced (Whitney et al 1993). Salmon populations experience high mortality rates as juveniles in freshwater, the estuary and early ocean, leading researchers to suggest that reducing mortality during these stages has the potential to substantially increase population growth rates (Kareiva et al. 2000). Although significant mortality of juvenile salmon and steelhead occur in the ocean, our ability to influence ocean survival is limited. Therefore, improvements in freshwater survival and production are imperative and can directly affect the number of returning adult salmon and steelhead (Raymond 1988, Beamesderfer et al. 1996).

Many of the measures taken to restore anadromous salmonid production in the Columbia River Basin have focused on improving the survival of juvenile migrants through the mainstem dams. Various life-cycle models indicate that mortality of juveniles during migration in freshwater constrains anadromous salmonid production in the Columbia River Basin, thereby reducing the benefits of enhancement measures upstream (Beamesderfer et al 1996, Kareiva 2000).

Increasing populations of piscivorous birds (primarily Caspian terns) nesting on islands in the Columbia River estuary annually consume large numbers of migrating juvenile salmonids (Ruggerone 1986; Roby et al. 1998) and thus constitute one of the factors that currently limit salmonid stock recovery (Roby et al. 1998; Independent Multidisciplinary Science Team 1998; Johnson et al. 1999). Therefore, reducing Caspian tern predation in the estuary, is one potential mechanism to increase population growth rates Endangered Species Act (ESA) listed salmonid Evolutionarily Significant Units (ESUs)[1] in the Columbia River Basin.

Anthropogenic changes in the Columbia River Basin appear to have facilitated increases in populations of colonial waterbirds (Roby et al. 1998). The largest recorded colony of Caspian terns in the world (Roby et al. 1998) now occupies an island created by dredging (and maintaining) a navigation channel in the Columbia River estuary. There, they feed primarily on large numbers of migrating juvenile salmon and steelhead. Basinwide losses to avian predators now constitute a substantial proportion of individual salmonid runs (Roby et al. 1998).

In the early 1990s, National Marine Fisheries Service (NMFS) staff at the Point Adams Field Station noted substantial increases in the size of newly established Caspian tern nesting colonies (Figure 1) on man-made islands in the Columbia River estuary (Figure 2). Several estuary islands on which piscivorous birds nest were created from materials dredged to maintain the Columbia River Federal Navigation Channel. There were no terns nesting in the Columbia River estuary before 1984 when about 1000 pairs apparently moved from Willapa Bay to nest on newly deposited dredge material on East Sand Island. Those birds moved to Rice Island in 1987. The number of Caspian terns nesting in the estuary has since expanded to 9,000-10,000 pairs (the largest colony ever reported). In 1999, the colony was encouraged to relocate to East Sand Island and, in 2001, the majority of the West Coast population nested on just two acres on East Sand Island.

Because of the growing concern over the increasing impacts of avian predation on salmonid smolts, NMFS required the Bonneville Power Administration (BPA) and U.S. Army Corps of Engineers (COE) to conduct an analysis of avian predation in the Columbia River estuary and (if necessary) to develop potential measures for managing the predator populations. These requirements were part of the 1995 Formal Consultation on the Operation of the Federal Columbia River Power System and Juvenile Transport Program (NMFS 1995). Oregon State University and the Columbia River Inter-Tribal

[1] Under the Endangered Species Act, the NMFS lists species, subspecies and distinct population segments of vertebrates. The NMFS policy stipulates that a salmon population will be considered distinct if it represents an “evolutionary significant unit” (ESU) of the biological species (Waples 1991). For the purposes of conservation under the ESA, an Evolutionarily Significant Unit (ESU) is a distinct population segment that is substantially reproductively isolated from other conspecific population units and represents an important component in the evolutionary legacy of the species (Waples 1991).

Fish Commission began conducting the research in 1996. The concern over large losses of salmonid smolts to newly established and rapidly expanding populations of avian predators stems from the fact that currently 12 ESUs of anadromous salmonids native to the Columbia River Basin are listed as threatened or endangered under the ESA (Figures 3 and 4).

NMFS, COE, FWS, BPA, Columbia River Inter-Tribal Fish Commission, and the resource agencies of the states of Washington and Oregon formed the Caspian Tern Working Group (CTWG) to develop a long-term management plan for reducing tern predation in the estuary. As part of this effort, the CTWG is testing the idea that terns can be dispersed to good habitat outside the Columbia River Basin without affecting their overall survival. In addition, NMFS is evaluating the overall risk tern predation presents to listed salmonid populations.

Caspian terns (*Sterna caspia*)

Caspian terns are highly migratory and exhibit cosmopolitan distribution (Harrison 1983; Harrison 1984). Caspian terns worldwide are expanding in range and numbers. Nesting has been reported from Baja California to the Bering Sea, from the Gulf Coast of Texas to Lake Athabaska, and from the Florida panhandle to Labrador - as well as in Australia, New Zealand, South Africa, Asia, and Europe. The West Coast population winters in Southern and Baja California and returns north to nest (Harrison 1983; Harrison 1984). Early colony size estimates in the Pacific Northwest showed as many as 500 pairs mixed with gulls and cormorants as far north as Klamath Lakes in Oregon (Harrison 1984). Some nesting colonies were first discovered in Washington near Moses Lake and Pasco in the 1930s, but coastal nesting was not recorded until 1958, when a colony nested in Grays Harbor (Penland 1976, 1981). Since the early 1960s, the population has shifted from small colonies nesting in interior California and Southern Oregon to large colonies nesting on human-created habitats along the coast (Gill and Mewaldt 1983). The current population in the Columbia River Basin is part of a dramatic north- and coastward expansion in the range and an overall increase in Caspian tern numbers in western North America.

The numbers of Caspian terns in western North America more than doubled between 1980 and 1999 (Cuthbert and Wires 1999). In the Columbia River estuary numbers of Caspian terns have increased from a few scattered individuals before 1984 to more than an estimated 20,000 in 2000 (Figure 1). The populations are continuing to expand, and the 2001 fledgling production from the East Sand Island colony in the Columbia River estuary was approximately equal (12,000 birds) to the West Coast adult population in 1980 (Collis et al. 2001a, Gill and Mehwaldt, 1983). A reason for this increase is that human-created habitat provides high quality nest sites and is associated with population increases throughout North America (Cuthbert and Wires 1999).

Caspian terns arrive in the Columbia River estuary in April and begin nesting at the end of the month (Roby et al. 1998). To avoid predators, terns construct their nests on islands (Harrison 1984) and show a preference for barren sand. They are piscivorous in nature (Harrison 1984), requiring about 220 grams (roughly one-third of their body weight) of fish per day during the nesting season. The timing of courtship, nesting and chick rearing corresponds with the outmigration of many of the salmonid stocks in the basin (Collis et al in press) (Figure 5).

Predation impacts

Two approaches have been taken to evaluate the extent of salmonid mortality resulting from Caspian tern predation. Since 1997, biologists with the BPA funded research project ("Avian Predation on Juvenile Salmonids in the Lower Columbia River," - a joint project of Oregon State University, U.S. Geological Survey, Columbia River Inter-Tribal Fish Commission, and Real Time Research Consultants) have observed salmonid mortality at tern colony sites and utilized a bioenergetics model[2] to provide estimates of mortality. The second approach is analyses of passive integrated transponders (PIT) tags detected on the tern colonies to determine salmonid predation rates by ESU (Collis et al.2001b, Ryan et al 2001).

Salmon constitute a major portion of tern diets in the estuary. The BPA funded research project initially estimated an annual loss of 4.75 to 14.5 million smolts attributable to the single Caspian tern colony in the estuary since 1997. Diet analyses in 1997 showed that juvenile salmonids constituted 75% of the food consumed by the Rice Island colony (Roby et al. 1998). During the peak of the yearling chinook salmon, coho salmon and steelhead smolt migration, which coincides with the peak of nesting activity in May, the diet of Caspian terns on Rice Island was 98% salmonid smolts (Roby et al 1998).

This concentration on smolts as a food source translates into a substantial predation rate during the salmonid outmigration period. Roby et al (1998) used the bioenergetics model to estimate that of the 70-80 million smolts entering the estuary in 1998, Caspian terns nesting on Rice Island consumed 6.6 to 24.7 million salmonid smolts (8-30% of all smolts). Further refinement of the bioenergetics model has modified some of the earlier estimates of smolt consumption. Best estimates of smolts consumed since 1997 are found in Table 1.

In 1997 and 1998, between one and two million salmonid smolts listed under the ESA entered the Columbia River estuary. This was about one or two percent of the total of all salmonid smolts in the estuary. However, in 1999, seven more ESUs of anadromous salmonids in the Columbia River Basin were listed, and roughly 6 million listed smolts

[2]A description of the bioenergetics model used to develop the estimate may be found in Roby et al. (1998).

entered the estuary along with 70 to 80 million unlisted smolts (primarily of hatchery origin). The majority of juvenile salmonids in the estuary are of hatchery origin and the majority being consumed by Caspian terns are hatchery fish (Independent Multidisciplinary Science Team 1998).

Table 1. Estimates of juvenile salmonids (in millions) consumed by Caspian terns in the Columbia River estuary 1997-2001[3].

Year	Number of Smolts Consumed (95% confidence interval in parentheses)
1997	7.48 (5.36 - 9.6)
1998	11.2 (8.3 - 14.2)
1999	11.7 (9.4 - 14.0)
2000	7.3 (6.1 - 8.6)
2001	5.9 (4.8 - 7.0)

Since 1987, researchers in the Columbia River Basin have placed over five million PIT tags in juvenile salmonids for various studies (Ryan et al 2001). Identifying PIT tags on Rice and East Sand Islands can provide a minimum estimate of proportion of the stocks that were consumed by terns in these colonies. Recently approximately one million juvenile salmonids are PIT tagged annually (Collis et al 2001b)[4]. Using tag detection equipment, over 115,000 PIT tags were detected on Rice Island in 1998 and 1999 (Ryan et al 2001). Collis et al (2001b) indicate that the majority of the 115,000 PIT tags detected were chinook salmon, steelhead, coho salmon and sockeye salmon. Of the PIT tags in steelhead tagged in 1997, that were detected at Bonneville Dam and subsequently detected on Rice Island, 2.8% were from wild stocks and 5.4% from hatchery stocks (Collis et al 2001b). For those steelhead PIT-tagged in 1998 and subsequently found on Rice Island, 11.7% were wild stocks and 13.4% were hatchery stocks (Collis et al 2001b). For yearling chinook salmon PIT-tagged in 1998, that were detected at Bonneville Dam and subsequently detected at Rice Island, 0.5% were wild stocks and 1.6% were hatchery stocks (Collis et al 2001b).

Ryan et al (2002 in review), analyzing PIT tag data from 1998 to 2000 on Rice Island and East Sand Island, determined that steelhead salmon experienced higher predation rates (0.6% to 10.6% on East Sand Island and 2.1% to 11.2% on Rice Island) than for chinook salmon (0.3% to 2.3% on East Sand Island and 0.6% to 2.3% on Rice Island). This supports the hypothesis of Collis et al (2001b) that size selectivity may be a key factor in why steelhead are more vulnerable than yearling chinook salmon.

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[3] Collis et al 2001a.

[4] The vast majority of PIT- tagged juvenile salmonids are from Snake River ESUs, primarily steelhead and chinook.

There are some important uncertainties and findings derived from estimating predation rates of salmon by Caspian terns. First, predation impacts derived from PIT tags represent a minimum estimate of proportion of the stocks that were consumed because an unknown number of tags are regurgitated or defecated off the colony site, wind and water erosion removes an unknown number, some tags may have been damaged and not detectable by the equipment, and not all tags are detected (Collis et al 2001b, Collis et al in press). Secondly, predation rates vary annually and by the methodology used to make the estimate, making it difficult to derive a single predation rate. Although there is good correspondence of predation rates between methodological estimates, utilizing the upper and lower bounds of the predation rates represent the most reliable rates that should be used to assess potential impacts of smolt predation by Caspian terns. Finally, it is clear that predation rates are not uniform for all salmon species, thus evaluation of the impact of Caspian tern predation should be salmon species specific, to the extent possible.

NMFS has developed a life cycle model - under the auspices of the Cumulative Risk Initiative at the NWFSC - to assess salmonid population trends and the impact of an anthropogenic activity on those trends (Appendix 1). The effort is applicable when mortality rates can be constructed and attributable to a particular activity. Assessing the impact of predation by Caspian terns on juvenile salmonids during a particular life history phase is amenable to such an evaluation.

Evaluation of salmonid mortality through the two methods described above varies inter-annually and between methods. Analysis of PIT tag data also indicate that the impact varies by species, with steelhead being the most impacted and yearling chinook salmon the least (Ryan et al. 2002 in review). The variability in predation rates make a definitive rate hard to determine. Therefore, we have developed a family of curves that bracket the estimated predation rates as part of the life-cycle model to estimate the impact of predation on population growth rates by species.

Estimates of Caspian tern predation rates have ranged from approximately less than 0.5%, for wild yearling chinook salmon, using PIT-tag recoveries on Rice Island to approximately 14% for steelhead (Ryan et al. in review). Using Equation [3] (Appendix 1), these mortality rates yield a maximum potential improvement in population growth rate of 0.2-2.3 % if this mortality could be completely eliminated (Table 2 and Figure 6). If mortality is reduced 50%, the impact on ESU specific population growth rate would improve approximately 0.1-1.0% (Table 3). Clearly, the magnitude of potential improvement to the population growth rate is dependent upon the degree to which mortality can be reduced (Tables 2 and 3 and Figure 6).

For comparative purposes, changes called for in NMFS' Biological Opinion on operation of the hydropower system (FCRPS), to improve passage for both adults and juveniles are anticipated to increase population growth rates by approximately 1-2 % for the Snake River Spring/Summer-run chinook salmon ESU and nearly 5% for the Snake River Fall-run chinook salmon ESU (NMFS, 2000). Harvest on the Snake River summer/chinook

ESU consists only of a minimal tribal ceremonial and subsistence harvest; eliminating it altogether would improve population growth rate by 1-2% (McClure et al., in review). The Upper Columbia River Spring-run chinook salmon ESU has similarly low harvest rates, but several other ESUs have sustained higher harvest rates and consequently benefit more from harvest reduction.

Several factors must be kept in mind when interpreting the results of these calculations, however. Perhaps the most important factor is that this type of calculation assumes that there is no compensatory mortality later in the life cycle, and that any reduction in tern predation is fully realized. In addition, from a management perspective, these results may not be as easy to achieve as they are to calculate. For instance, the relationship between tern abundance and predation rate is not well known, which makes it difficult to directly relate a change in colony size to a change in predation rate.

Nonetheless, results obtained by running this model strongly support the hypothesis that predation of juvenile salmonids affects the survivability of salmonid populations. This is especially true for upper river stocks of steelhead.

Relocation Efforts

In 1999, 2000 and 2001, efforts to relocate the terns to East Sand Island were undertaken. These efforts have apparently been successful in reducing predation on smolts without affecting tern productivity[5]. Caspian tern diets of almost exclusively salmonids at Rice Island (77% and 90% in 1999 and 2000) shifted to 46%, 47% and 33% salmonids at East Sand Island in 1999, 2000 and 2001 respectively (Collis et al 2001a, Roby et al in press). This represents substantial declines in juvenile salmonid mortalities. The effort to relocate terns resulted in a significant reduction in the number of salmon consumed per pair of terns on East Sand Island compared to tern pairs on Rice Island in 1999 and 2000 (Ryan et al 2002 in review). In 2000, smolt consumption was estimated at 7.3 million, a 4.4 million reduction compared to 1999 - the last time terns nested on Rice Island (Collis et al 2001a, FWS 2001). Consumption of salmonid smolts in 2001 was estimated at 5.9 million - a 5.9 million reduction compared to 1999 (Collis et al 2001a). In addition, Caspian tern productivity at East Sand Island in 2001 was the highest recorded for terns nesting in the estuary (Collis et al 2001a). It is apparent that relocating terns to a habitat that offers a greater diversity of prey resources reduces the predation impact to juvenile salmon.

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[5] The CTWG relocated the Caspian tern colony from Rice Island to East Sand Island in an attempt to decrease salmonid losses by moving the tern colony to a site with abundant alternate prey sources. Over the last two years, with abundant alternate prey species, predation on salmonids was less than previous years. Nesting success has been substantially higher for Caspian terns nesting on East Sand Island as compared to Rice Island (Roby et al in press). Relocating the colony to the lower island, which is closer to the periodically abundant clupeids, has contributed to the reduction.

Conclusion

The ecosystem inhabited by anadromous salmonids is extensive and complex. In the case of upper Columbia River and Snake River salmon and steelhead, the ecosystems extend inland as far as 1500 km and rise to elevations of 2500 m above mean sea level. The oceanic portion these species inhabit extends through the North Pacific Ocean to the Bering Sea and the Sea of Japan. Human activities have had adverse affects on water flows, migration corridors, spawning and rearing habitat and eventually, salmonid survival and productivity. Wild and naturally reproducing stocks of steelhead have declined dramatically in the interior Columbia River Basin (Lee et al. 1997). Wild and naturally reproducing spring- and summer-run chinook stocks also have declined dramatically throughout the Pacific Northwest. As a result, nearly every population of naturally producing anadromous salmonids in the Columbia River Basin is now listed (or is a candidate for listing) under the ESA.

Not all listed salmonid populations have declined because of the same factors or combination of factors, and not all populations could be expected to respond positively to any particular management measure or combination of measures. However, any change in the freshwater ecosystem that moves the ecosystem away from a natural or "normative" condition is likely to be detrimental, just as any change that moves the ecosystem toward the normative condition is likely to elicit a positive population response from the listed species.

In the case of the avian predator populations discussed here, the non-normative condition is the creation of islands that would not be expected in the natural ecosystem because of the geology and hydrology of the river. Artificial islands (such as Rice Island), in turn, have promoted the development of unprecedentedly large colonies of piscivorous birds with subsequent increases in losses of juvenile salmonids from predation.

Evaluations of salmonid predation by Caspian terns indicate that substantial numbers of juvenile salmonids are being consumed. Two approaches to evaluate the extent of that impact yield similar results, steelhead are substantially impacted by tern predation while yearling chinook are not as impacted. Efforts to reduce predation by moving the colony from Rice Island to East Sand Island have successfully decreased overall predation. However, PIT-tag data from East Sand Island indicate that there is still a substantial impact on salmonids (steelhead). Based on these results, NMFS is still concerned about the extent of predation on salmonids, and in particular to steelhead, resulting from predation by Caspian terns. It is difficult to determine exactly what population level of birds within the estuary would provide the greatest benefit to fish without unduly impacting the terns. Therefore, NMFS believes that it is important to pursue a long term strategy to disperse the birds to a broader and more extensive array of habitats that offer a diversity of prey resources.

One possible scenario is to work towards modifying the estuary to resemble historic natural habitats. Natural river islands are either sand and gravel bars that flood at high tide or during high flows in spring freshets or islands that have existed above the water surface long enough to develop normal, diverse, native, vegetative and animal communities. While these islands were in the process of vegetating, small mobile colonies of various ground nesting birds would use them until encroaching vegetation excluded them from nesting. Caspian terns historically have exhibited the ability to quickly respond to changes in nesting habitat (Gill and Mewaldt 1983). The relatively recent shift away from many small colonies of Caspian terns to fewer and larger colonies is an apparent response to losses of historic breeding habitats and the construction of habitat elsewhere. Huge colonies of ground-nesting piscivorous birds are not a historic component of the ecosystem of Columbia River estuary because extensive habitat was not available. However, complete removal of the population of Caspian terns from the estuary will not in itself recover listed stocks.

Return of the nesting islands to a normative condition in the estuary would require years of physical habitat changes and establishment of native flora and fauna. During this period, the populations of predatory birds would be able to adjust to an ecologically normative level that could be supported on the existing habitat.

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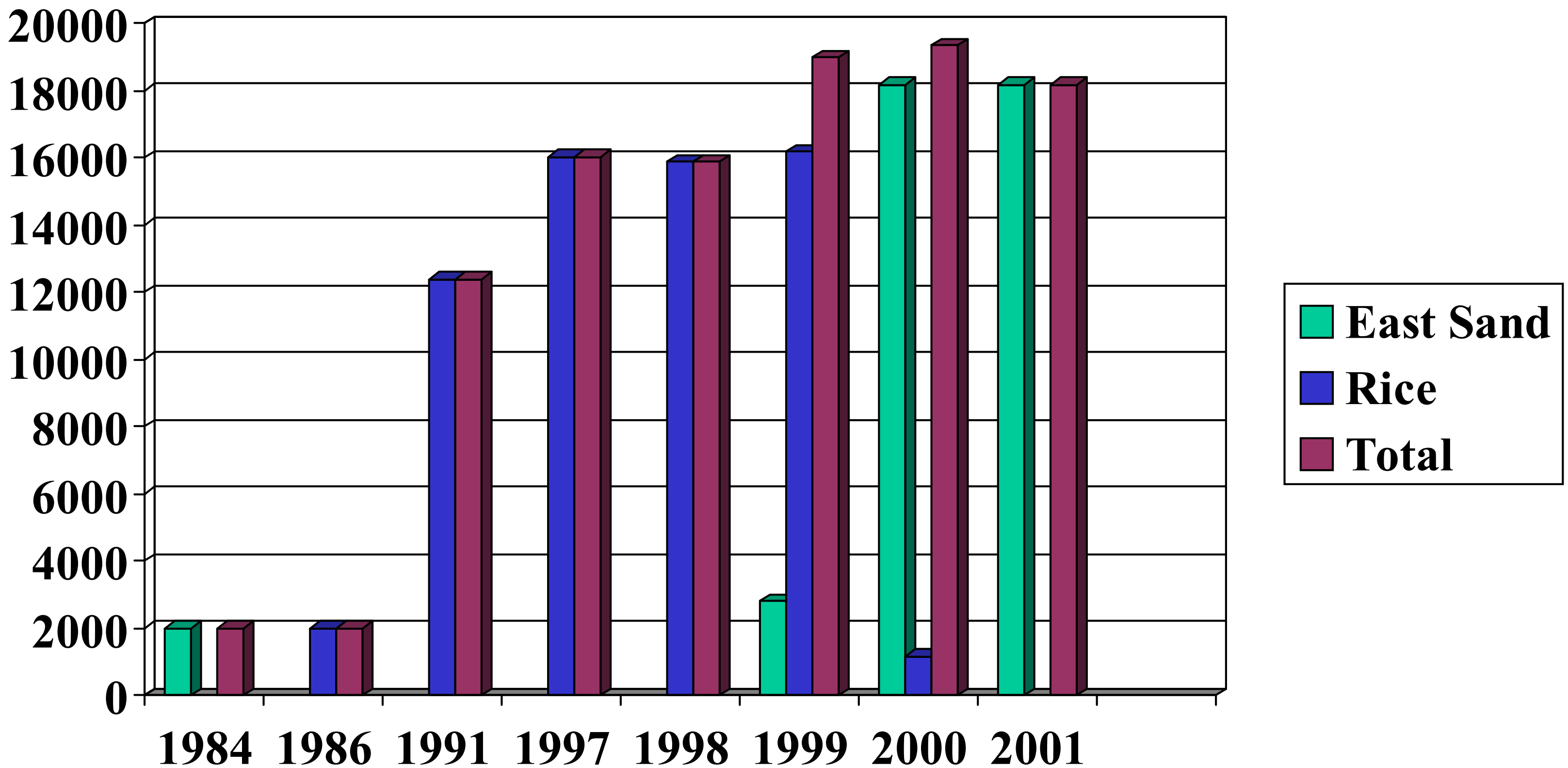

Figure 1. Numbers of Caspian terns utilizing islands in the Columbia River estuary for nesting since 1984.

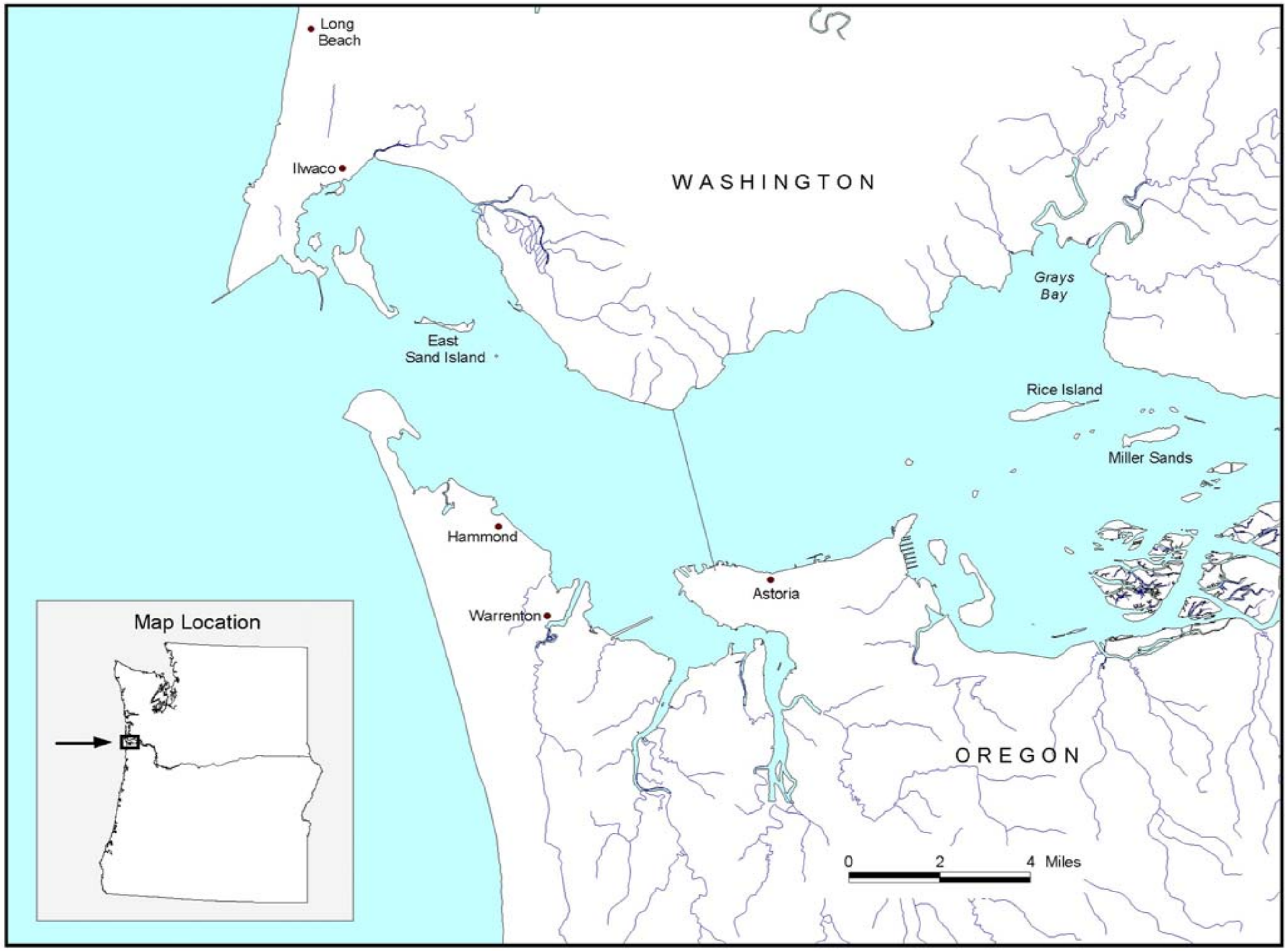

Figure 2. Map of the Columbia River estuary showing the relative locations of East Sand and Rice Islands, sites of Caspian tern nesting colonies.

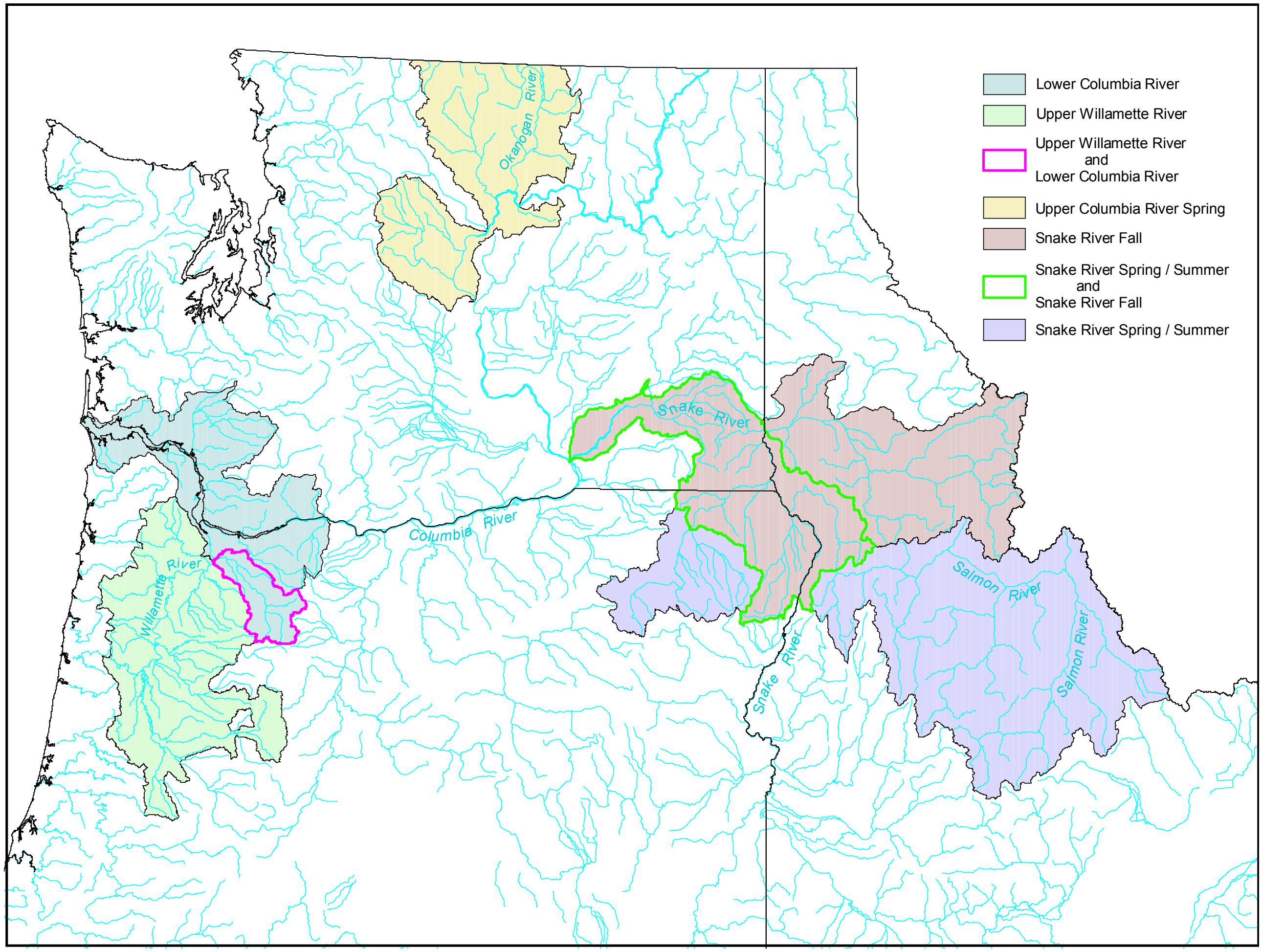

Figure 3. Map of Columbia River Basin listed chinook salmon ESUs.

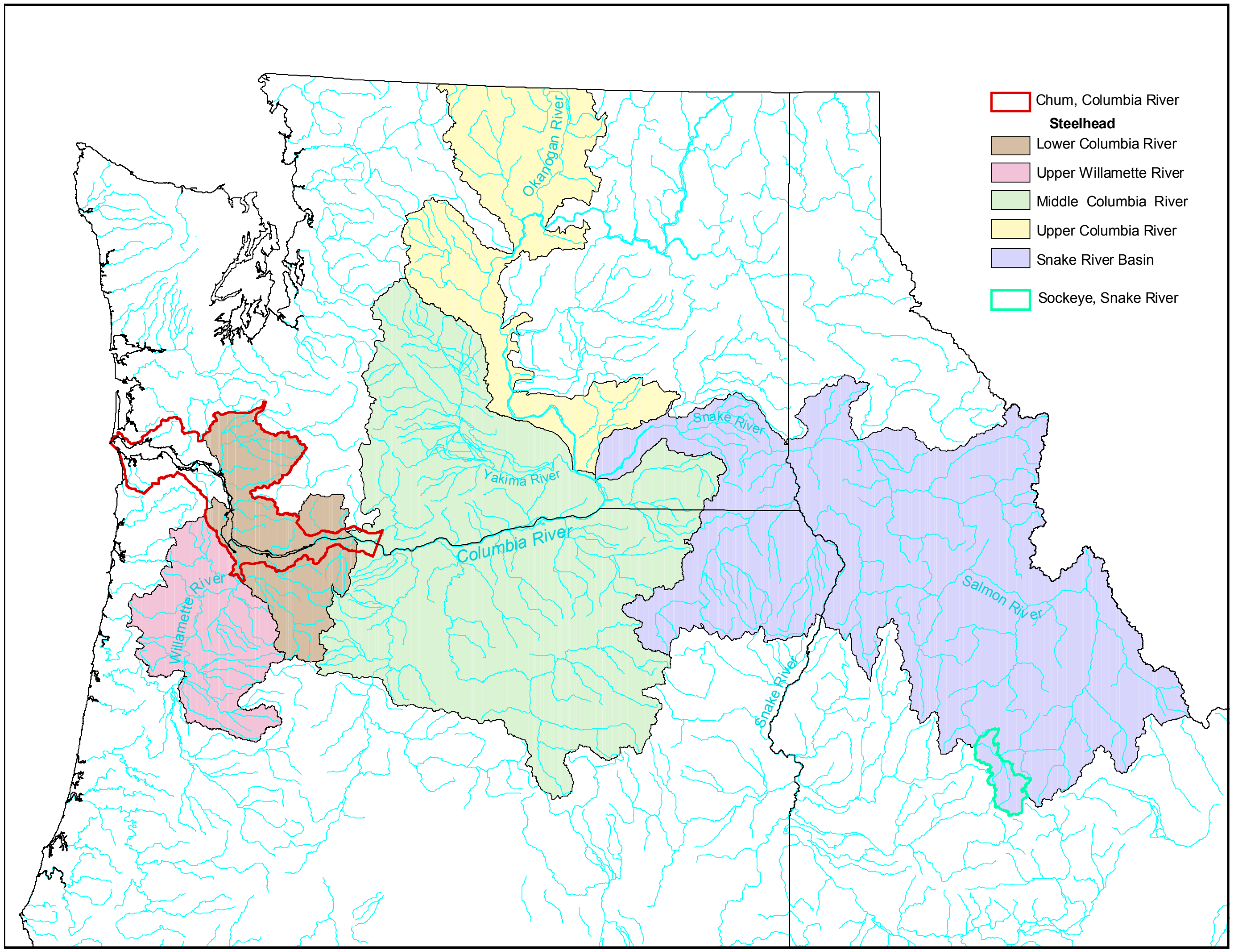

Figure 4. Map of the Columbia River Basin listed steelhead, sockeye and chum salmon ESUs.

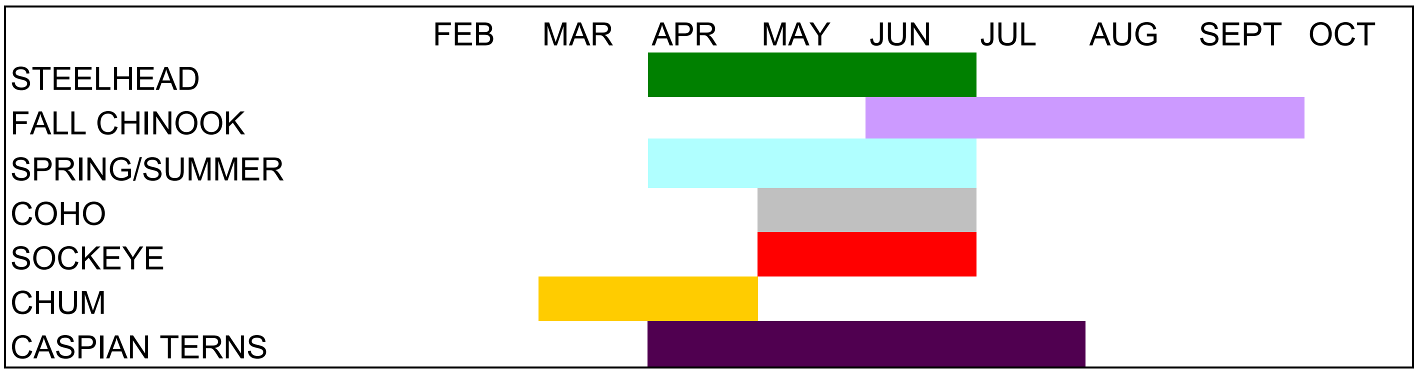

Figure 5. Arrival times of juvenile salmonids and nesting period of Caspian terns in the Columbia River estuary.

Table 2. Estimated percent change in population growth rate with the complete elimination of tern predation of varying rates for listed salmonid ESUs in the Columbia River Basin.

Predation Rate	Snake River spring/summer chinook	Snake River Fall Chinook	Snake River Steelhead	Upper Columbia Chinook	Upper Columbia Steelhead	Mid-Columbia Steelhead	Upper Willamette Chinook	Upper Willamette Steelhead	Lower Columbia Chinook	Lower Columbia Steelhead	Columbia River Chum
1.0%	0.234	0.274	0.210	0.236	0.267	0.207	0.227	0.247	0.298	0.217	0.279
2.5%	0.591	0.692	0.530	0.595	0.675	0.523	0.573	0.622	0.752	0.548	0.704
5.0%	1.201	1.407	1.077	1.208	1.372	1.063	1.165	1.265	1.529	1.114	1.431
6.1%	1.476	1.730	1.323	1.485	1.686	1.306	1.431	1.555	1.880	1.369	1.759
9.3%	2.298	2.695	2.059	2.312	2.627	2.033	2.228	2.421	2.930	2.131	2.741
10.0%	2.482	2.912	2.224	2.498	2.839	2.196	2.407	2.616	3.166	2.302	2.962
20.0%	5.330	6.269	4.769	5.365	6.108	4.708	5.166	5.622	6.825	4.938	6.376
Generation Time	4.297	3.67	4.79	4.27	3.764	4.85	4.43	4.08	3.38	4.63	3.61

Table 3. Estimated percent change in population growth rate with a 50% reduction in tern predation, given current predation of varying rates for listed salmonid ESUs in the Columbia River Basin.

Predation Rate	Snake River spring/summer chinook	Snake River Fall Chinook	Snake River Steelhead	Upper Columbia Chinook	Upper Columbia Steelhead	Mid-Columbia Steelhead	Upper Willamette Chinook	Upper Willamette Steelhead	Lower Columbia Chinook	Lower Columbia Steelhead	Columbia River Chum
1%	0.117	0.137	0.105	0.117	0.133	0.103	0.113	0.123	0.148	0.108	0.139
2.50%	0.297	0.343	0.263	0.295	0.335	0.260	0.284	0.309	0.373	0.272	0.349
5%	0.606	0.692	0.530	0.595	0.675	0.523	0.573	0.622	0.752	0.548	0.704
6.10%	0.747	0.848	0.649	0.728	0.826	0.641	0.702	0.762	0.921	0.671	0.862
9.30%	1.170	1.306	0.999	1.121	1.273	0.987	1.081	1.174	1.419	1.034	1.328
10%	1.266	1.407	1.077	1.208	1.372	1.063	1.165	1.265	1.529	1.114	1.431
20%	2.779	2.912	2.224	2.498	2.839	2.196	2.407	2.616	3.166	2.302	2.962
Generation Time	4.297	3.67	4.79	4.27	3.764	4.85	4.43	4.08	3.38	4.63	3.61

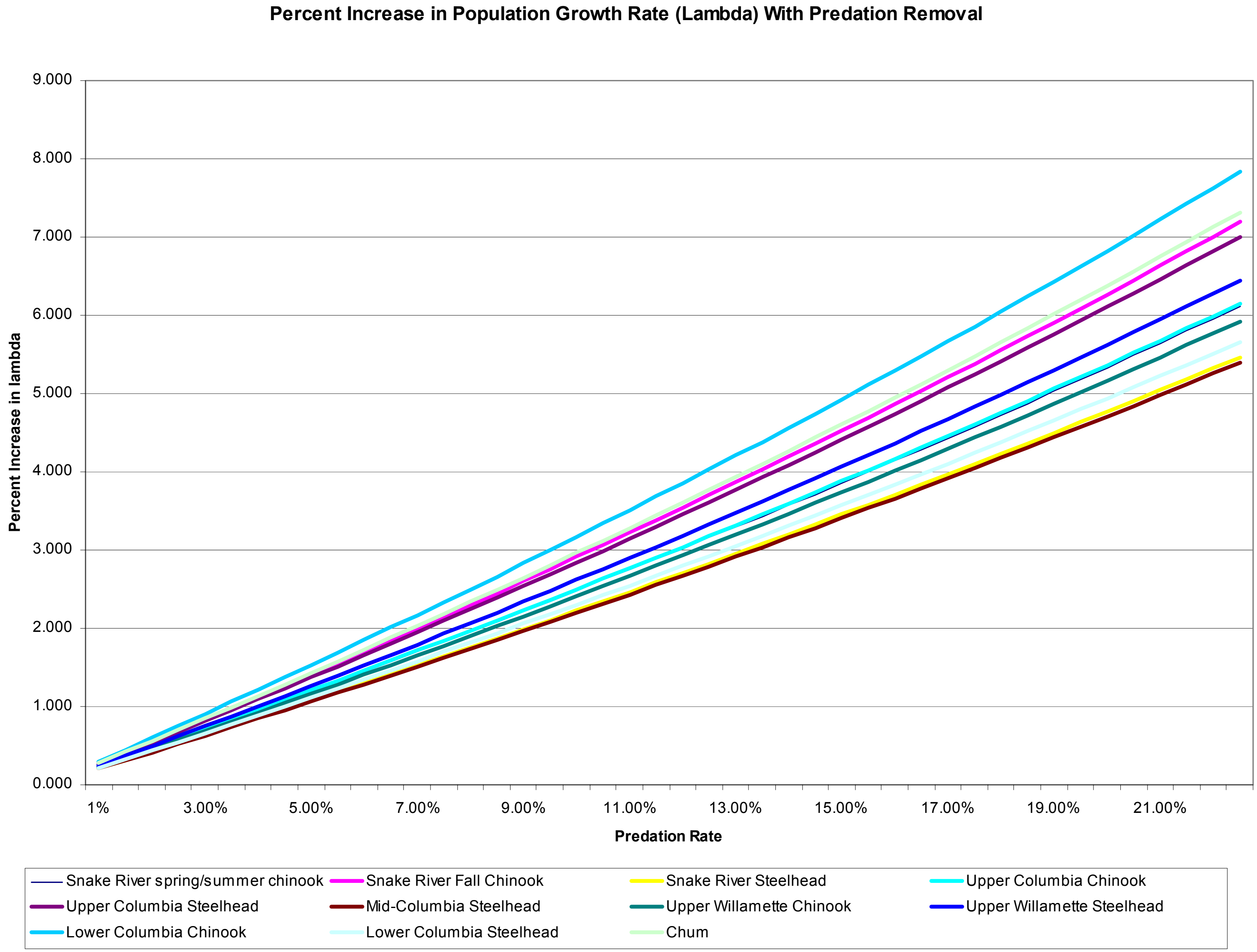

Figure 6. Percent increase in population growth rate (Lambda) with Caspian tern predation removal

Appendix 1

Cumulative Risk Initiative

The total survival rate for any population, across its entire life cycle is the combined survival rates across all life stages:

$$S_t = S_1 * S_2 * S_3 * \ldots * S_n \qquad [1]$$

where S_t is the total (life cycle) survival rate, n is the number of stages into which the life cycle has been divided, and S_n is the survival rate at each stage. The adult-to-adult ratio (or recruits per spawner, *R/S*, for salmonids) is merely the life-cycle survival multiplied by the mean fecundity. If the organisms in question are annuals, this is also the annual rate of population change (Caswell, 2000). For longer-lived species, such as salmonids, it can be approximated as follows:

$$= R/S^{\,1/generation\ time} \qquad [2]$$

This equation annualizes the adult-to-adult ratio, and provides equivalent metrics for comparison between species (or ESUs) with different generation times.

Because the total life cycle survival is the product of all life-stage survivals, calculating the proportional change in population growth rate due to a change in survival rate at a single stage is straightforward:

$$P = \left(\frac{S_{new}}{S_{old}}\right)^{1/gentime} \qquad [3]$$

$$P = \left(\frac{S_{new}}{S_{old}}\right)^{1/gentime}$$

where P is the proportional change, S_{new} is the new (changed) survival rate, S_{old} is the original survival rate, and *gentime* is the generation time.